Exercise tolerance during muscle contractions below and above the critical torque in different muscle groups

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<tr>
<th>Journal:</th>
<th>Applied Physiology, Nutrition, and Metabolism</th>
</tr>
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<tr>
<td>Manuscript ID</td>
<td>apnm-2017-0381.R2</td>
</tr>
<tr>
<td>Manuscript Type:</td>
<td>Article</td>
</tr>
<tr>
<td>Date Submitted by the Author:</td>
<td>24-Sep-2017</td>
</tr>
<tr>
<td>Complete List of Authors:</td>
<td>Abdalla, Leonardo; Human Performance Laboratory Denadai, Benedito; UNESP, Bassan, Natalia; Human Performance Laboratory Greco, Camila; Human Performance Laboratory,</td>
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<td>Is the invited manuscript for consideration in a Special Issue? :</td>
<td></td>
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<tr>
<td>Keyword:</td>
<td>exercise, isometric, maximal voluntary contraction, fatigue, exercise intensity domain</td>
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Exercise tolerance during muscle contractions below and above the critical torque in different muscle groups

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Abstract

The objective of this study was to test the hypotheses that end-test torque (ET) (expressed as % maximal voluntary contraction - MVC) is higher for plantar flexors (PF) than knee extensors (KE) muscles, whereas impulse above ET (IET) is higher for KE than PF. Thus, we expected that exercise tolerance would be longer for KE than PF only during the exercise performed above ET. After the determination of MVC, forty men performed two 5-min all-out tests to determine ET and IET. Eleven participants performed a further four intermittent isometric tests, to exhaustion, at ET + 5% and ET - 5%, and one test for KE at the exercise intensity (%MVC) corresponding to ET + 5% of PF. The IET (7243.2 ± 1942.9 vs. 3357.4 ± 1132.3 Nm s) and ET (84.4 ± 24.8 vs. 73.9 ± 19.5 N m) were significantly lower in PF compared with KE, respectively. The exercise tolerance was significantly longer for PF (300.7 ± 156.7 s) than KE (156.7 ± 104.3 s) at similar %MVC (~60%), and significantly shorter for PF (300.7 ± 156.7 s) than KE (697.0 ± 243.7 s) at ET + 5% condition. However, no significant difference was observed for ET - 5% condition (KE = 1030.2 ± 495.4 s vs. PF = 1028.3 ± 514.4 s). Thus, the limit of tolerance during submaximal isometric contractions is influenced by absolute MVC only during exercise performed above ET, which seems to be explained by differences on both ET (expressed as %MVC) and IET values.

Key words: maximal voluntary contraction, exercise, isometric, muscle volume, fatigue, exercise intensity domain.
Introduction

Exercise tolerance during different high intensity exercise protocols (i.e., constant work rate, incremental, self-paced and all-out) can be predicted by a hyperbolic work rate/time function (i.e., critical power model) (Chidnok et al. 2013; Souza et al. 2015). Using this function, it is possible to estimate both the critical power (the asymptote of the power/time hyperbola) and the hyperbola’s curvature constant (W’) (Dekerle et al. 2015). Critical power has been considered the lower boundary of severe intensity domain and corresponds to the highest sustainable rate of oxidative metabolism. The W’ represents the total amount of work that can be performed above critical power before exhaustion occurs.

Traditionally, critical power and W’ and those equivalent for running and swimming (critical velocity and D’, respectively), have been estimated by 3-5 high-intensity constant work-rate exercises (Jones et al. 2010). Aiming to reduce the number of bouts of exhaustive exercise, Vanhatalo et al. (2007) demonstrated that the parameters of critical power model can be estimated by a single 3-min all-out exercise test. In this protocol, the end-test power (the power output in the last 30 s of the test) and the work done above end-test power were similar to the parameters (critical power and W’, respectively) estimated during the conventional protocol (i.e., constant work-rate exercises).

Recently, some studies have utilized 5-min all-out intermittent isometric single-leg knee-extensor exercise to characterize muscle bioenergetics and fatigue (Burnley et al. 2012; Broxterman et al. 2017). Moreover, this protocol has been utilized to estimate the critical force / torque during exercise involving
different muscle groups (e.g., knee extensors and forearm flexors) (Burnley 2009; Kellawan and Tschakovsky 2014). Interestingly, the intramuscular metabolic response and the torque vs. time shape curve are similar to that observed during the 3-min all-out cycling exercise (Burnley et al. 2012; Broxterman et al. 2017).

Indeed, Burnley (2009) verified that the end-test torque (ET) during 5-min all-out knee extensor protocol is similar to the asymptote of the torque-duration relationship (i.e., critical torque). In line with this data, Kellawan and Tschakovsky (2014) have shown that the parameters estimated during this protocol presented an excellent repeatability (ET, ICC = 0.94) and are valid to predict the exercise tolerance during exercise at a constant intensity above the ET.

Submaximal isometric contraction (sustained or repeated) performed at a given % of an individual's maximum voluntary contraction (%MVC) has been extensively utilized to normalize the exercise intensity during different experimental designs and clinical settings (Frey Law et al. 2010; Millar et al. 2014). This paradigm assumes that both acute and chronic physiological responses to submaximal isometric contraction present a low inter individual variability. In addition, %MVC has also been utilized to compare acute response to submaximal isometric contraction involving different muscle groups. However, exercise tolerance during submaximal isometric contraction presents a high inter individual variability (Frey Law et al. 2010) and is proposed to be dependent on absolute force/muscle cross-sectional area (Hunter and Enoka 2001). Higher absolute force during isometric contraction is associated with partial occlusion of blood flow and impairment of oxygen delivery to the muscle. The O₂ delivery is
an important determinant of critical torque / force, and presumably, the exercise
tolerance during submaximal isometric contraction (Kellawan et al. 2014).
Notwithstanding, a greater absolute force/muscle cross-sectional area could be
associated with higher impulse accumulated above critical torque (IET) (Byrd et
al. 2017). In the critical torque model, IET is only utilized during exercise
performed above critical torque, and task failure at this intensity is associated
with its complete utilization (Dekerle et al. 2015). Thus, exercise tolerance during
submaximal isometric contraction would be better analysed using the critical
torque model, instead a given %MVC.

To date, the parameters of critical torque model obtained in muscle groups
with different absolute MVC values and their possible influence on exercise
tolerance has not been assessed within distinct exercise intensity domains. Thus,
the main objectives of this study were: a) to compare the parameters estimated
by the critical torque model between the knee extensors (KE) and plantar flexors
(PF) muscle groups; and b) to compare the exercise tolerance of the KE and PF
muscle groups during the exercise performed bellow (− 5%) and above (+ 5%)
ET. We hypothesized that: 1) the PF would present a higher ET (expressed as
%MVC) than KE; 2) the KE would present a higher IET than PF; 3) the exercise
tolerance during the exercise performed above ET (i.e., severe exercise domain)
will be higher for KE than PF, and; 4) the exercise tolerance will be similar
between PF and KE muscle groups during the exercise performed bellow ET.

**Methods**
**Subjects**

Forty active males (mean ± SD, 25.5 ± 5.0 years; 75.7 ± 15.0 kg; 175.5 ± 6.5 cm) volunteered to participate in the study. All participants were healthy and free of cardiovascular, respiratory, and neuromuscular diseases. All risks associated with the experimental procedures were explained before involvement in the study and each participant signed an informed consent form. The study was performed based on the Declaration of Helsinki, and the protocol was approved by the University’s Ethics Committee.

**Experimental design**

The participants were tested in a climate-controlled (21–23°C) laboratory at the same time of day (± 2 h) to minimize the effects of diurnal biological variation. In the first visit, each participant performed a familiarization session to the isokinetic dynamometer. On the following two visits, the participants performed maximal isometric voluntary contractions (MVC) of the KE and PF to determine isometric peak torque. After 30 min of rest, the participants performed a 5-min intermittent all-out test, to determine the ET and IET. The order of the two experimental sessions was randomized. Eleven participants performed a further five intermittent tests, to exhaustion, at different intensities, to determine the time limit. These tests were conducted at different days and the order of the intensities was randomized within the same muscle group. The interval between the experimental sessions was at least 48 h. The participants were instructed to arrive at the laboratory in a rested and fully hydrated state at least 3 h post-
prandial, and they were asked not to perform any strenuous activity during the
day prior to each test.

**Familiarization**

Familiarization involved maximal (5 min) and submaximal (10 min)
isometric voluntary contractions with 3-s duration, interspersed with 2 s of rest.
For the submaximal contractions the target torque was displayed on a screen.

**Maximal voluntary contraction**

For KE muscles, participants were placed in a sitting position and securely
strapped into the test chair, with the hip and knee joints at angles of 85° and 75°,
respectively. The joint angles were measured using a goniometer. Extraneous
movement of the upper body was limited by two cross-shoulder harnesses and
an abdomen belt. The axis of the dynamometer was aligned with the right knee
flexion-extension axis, and the lever arm was attached to the participant’s shank
with a strap. For PF muscles, the participants lay supine on the seat of the
dynamometer, with hip at 25º of flexion and the knee at full extension (0º) and
knee angles, and the ankle angle at 90º. The joint angles were measured using a
goniometer. Extraneous movement of the upper body was limited by two cross-
shoulder harnesses, and straps at the waist, the thigh, the shank and the foot.
The chair settings were recorded and replicated in all tests. Participants were
asked to relax their leg so that the effects of gravity on the passive limb and lever
arm could be measured. The warm-up of the isometric tests consisted of a set of
five submaximal isometric contractions, followed by 5-min rest. The peak torque measurement involved three isometric MVC of 3 s, separated by a rest period of 3 minutes. The test was performed in the dominant limb. The participants were instructed to perform a maximum effort for each trial, and strong verbal encouragement was provided by the researchers. The peak torque corresponded to the highest torque value attained during the trials.

**End-test torque and impulse above end-test torque**

A 5-min all out test was utilized to determine ET and IET of KE and PF. It consisted of 60 maximal intermittent isometric contractions (3 s exercise, 2 s rest) (Burnley 2009). Before the test, a 10-min warm-up was given, consisting of submaximal isometric contractions and MVC, followed by 5-min rest before the commencement of the test. The participants were informed about their MVC value measured during the warm-up period, and instructed to attain or exceed this value during the first 3-5 contractions of the test. During the whole test, they were strongly encouraged to perform the maximal effort at each muscle contraction, but not received information regarding the elapsed time and contractions remaining. The ET corresponded to the mean torque values of the last six contractions, and IET was estimated through to the area under the torque vs. time curve (Burnley 2009).

**Submaximal trials**
The constant-load intermittent tests to exhaustion were performed at ET + 5% and ET - 5% for both muscle groups, in random order. Additionally, another constant-load intermittent test to exhaustion was performed for KE muscle groups at the exercise intensity (i.e., %MVC) corresponding to the ET + 5% of the PF muscle group. During these tests, the individuals performed submaximal isometric contractions of 3 s interspersed with 2 s of recovery until task failure. The target torque was shown in the computer display screen with a red line. The participants were verbally encouraged to maintain the target torque in all contractions. The time of the first of three consecutive muscle contractions where the subject was unable to attain the target torque even with verbal encouragement corresponded to the time limit (Burnley 2009; Kellawan and Tschakovsky 2014) (Figure 1).

**Measurements**

The torque data were sampled at 1000 Hz (Miotec®, Porto Alegre/RS, Brasil) and were analyzed using algorithms written in Matlab (The MathWorks, Natick, MA, USA). The torque curves were smoothed by a digital fourth-order zero-lag Butterworth filter with a cutoff frequency of 20 Hz (Winter, 1990).

**Statistical analysis**

The data are presented as means ± SD. The normality of data was checked by the Shapiro-Wilk test. A Student t test for paired data was used to compare the variables MVC, ET, IET and time limit between the muscle groups.
The relationship between the time limit predicted from the critical power model and actual time limit was assessed using Pearson's product moment correlation coefficient. The significance level was set at $p < 0.05$ and effect sizes (ES) were calculated.

**Results**

**MVC and parameters of critical torque model**

The mean ± SD values of MVC, IET, and ET for KE and PF are shown in Table 1. The MVC (ES = 2.19), IET (ES = 2.44) and ET (ES = 0.47) were significantly lower in PF compared with KE ($p < 0.01$). However, the ET expressed as a percentage of MVC was significantly higher in PF (40.9 ± 7.7% MVC) than KE (29.0 ± 8.1% MVC) ($p < 0.01$; ES = 1.50). The IET/MVC was significantly smaller for PF compared with KE (PF = 17.7 ± 5.4 vs. KE = 22.4 ± 7.9, ES = 1.25). However, the ET/MVC was significantly greater for PF compared with KE (PF = 0.41 ± 0.08 vs. 0.29 ± 0.08, ES = 1.50). The mean torque profile of the 5-min test is shown in Figure 2.

There was significant correlation between IET and MVC for both KE ($r = 0.67$, $p < 0.05$) and PF ($r = 0.62$, $p < 0.05$) muscle groups. However, the correlation between ET and MVC was significant only for PF ($r = 0.71$, $p < 0.05$).

**Exercise tolerance**

The actual torque values performed during the exercise tolerance tests were 116 ± 15 N·m and 106 ± 14 N·m for ET + 5% and ET - 5%, respectively.
The actual torque performed during the exercise condition at the exercise intensity (i.e., %MVC) corresponding to the ET + 5% of the PF was 178.8 ± 34.8 N·m, and corresponded to 59 ± 8% MVC.

The mean ± SD values of the time limit obtained during the time exhaustion tests at ET + 5%, ET - 5% and %MVC are presented in Table 2. There was no significant difference between actual and predicted time limit for KE and PF at ET + 5% condition. Additionally, significant correlation between the actual and predicted time limit for both KE (r = 0.66) and PF (r = 0.72) was observed. The time limit at ET + 5% was significantly shorter for PF than KE (p < 0.001, ES = 1.93). However, the time limit of KE and PF was similar at ET - 5% condition (p = 0.45, ES = 0.01), but it was significantly longer for PF than KE at %MVC condition (p < 0.001, ES = 1.08).

Discussion

The main objectives of this study were to compare both the parameters estimated by the critical torque model and the exercise tolerance during exercise performed below and above ET in muscle groups with different MVC values (i.e., KE vs. PF). Consistent with previous research (Hunter and Enoka 2001), it was verified that exercise tolerance is dependent on absolute force (i.e., PF > KE) during severe-intensity exercise performed at similar %MVC (~ 60%). However, the main and original findings were as follows: (1) exercise tolerance is dependent on IET (i.e., KE > PF) when submaximal isometric contraction is performed at similar amplitude (5%) above ET; (2) exercise tolerance is
independent on absolute force when submaximal isometric contraction is performed at similar amplitude (5%) below ET; and (3) MVC explain, at least in part, both the inter individual variability and the difference observed in ET and IET of KE and PF. The main implication of these findings is that absolute MVC influences exercise tolerance during submaximal isometric contractions only when ET is exceeded.

Validity of 5-min all-out intermittent isometric

There is a substantial body of evidence indicating that a single 3-min all-out cycling test against fixed resistance is valid to estimate the parameters of critical power model (critical power and \( W' \)) determined during conventional protocol (i.e., constant work-rate exercises) (Vanhatalo et al. 2007; Vanhatalo et al. 2008). During this protocol, the finite work capacity is continuous utilized, such that the work done above EP is similar to \( W' \) and the power output plateau at critical power. Interestingly, the skeletal muscle bioenergetics (i.e., sources and rates of ATP synthesis) and the magnitudes of intramuscular metabolic perturbation (e.g., pH and \([\text{Pi}]\)) during 3-min all-out cycling exercise and 5-min all-out intermittent isometric exercise seems to be very similar (Broxterman et al. 2017). Thus, all-out intermittent isometric protocols seem to be an attractive approach to investigate the physiological response during a single test.

Few studies have analysed the validity of 5-min all-out intermittent isometric exercise to estimate the parameters determined during the critical torque / force model. Burnley (2009) verified that ET obtained during repeated
maximal isometric contractions of the KE was not different and significant correlated \( (r = 0.88, p = 0.004) \) with critical torque estimated from the impulse-time model. Using a different approach and muscle group (i.e., forearm flexors), Kellawan and Tschakovsky (2014) verified that the 5-min all-out intermittent isometric exercise is valid to estimate the parameters of critical torque model. In this study, time limit predicted by ET and IET showed a good agreement with actual time limit during exercise at a constant intensity above the ET \( (r = 0.97, p < 0.01) \). The data of the present study confirm and extend the validity of the 5-min all-out intermittent isometric protocol, since the actual time was not different and significantly correlated with time limit predicted by ET and IET, irrespectively of muscle group.

**Exercise tolerance across exercise intensity domains and muscle groups**

Traditionally, a given %MVC has been utilized to analyse the limit of tolerance during small-muscle-mass exercise (Frey Law et al. 2010). In this model, exercise tolerance has been inversely related with absolute force/muscle cross-sectional area (Hunter and Enoka 2001). Indeed, the present study found that exercise tolerance during similar repeated submaximal isometric contractions (i.e., \( \sim 60 \% \text{MVC} \)) was significantly longer for PF than for KE. Differences in blood flow occlusion and impairment of oxygen delivery to the muscle has been claimed as an important mechanism to explain the effect of absolute force/muscle cross-sectional area on exercise tolerance (Hunter and Enoka 2001). However, a different scenario emerges when the critical torque
model was utilized to compare the limit of tolerance between KE and PF. During repeated submaximal isometric contractions performed above ET (i.e., ET + 5%), KE presented a longer exercise tolerance than PF. Exercise tolerance during exercise performed above critical torque is influenced by both the magnitude of IET and the rate of its utilization (i.e., the exercise intensity amplitude above ET) (Dekerle et al. 2015). Indeed, different experimental design has confirmed that the size of the W' remains constant irrespective of its rate of expenditure, with task failure coinciding with consistently low values of muscle PCr and pH, and accumulation of fatigue-related metabolites (i.e., Pi, H+) (Vanhatalo et al. 2010). Thus, the higher magnitude of IET seems to explain the longer exercise tolerance of KE during exercise performed at similar amplitude above ET (i.e., > 5%). A different condition is presented when KE and PF were compared during similar repeated submaximal isometric contractions (i.e., ~ 60 %MVC). In this condition, KE performed the exercise at higher amplitude in relation to ET (KE = ET + 60% vs. PF = ET + 5%), and consequently, its higher magnitude of IET is not sufficient to determine similar time limit. Finally, exercise performed below ET is characterized by stable values for [PCr], [Pi], and pH with no substantial utilization of W' (Jones et al. 2008). Thus, exercise tolerance at this intensity is theoretically independent of IET magnitude. Indeed, time limit was not significantly different between KE and PF. The mechanism responsible for muscle fatigue during this exercise intensity is apparently more complex, and seems to be linked with both metabolic and ionic perturbation (Black et al. 2017).
MVC and parameters of critical torque model

Few studies have investigated the possible influence of neuromuscular characteristics on the parameters estimated from the critical power model. The present study verified that inter individual variability of IET was moderated explained by MVC. Moreover, both MVC and IET were significantly higher for KE than for PF, although IET normalized by MVC was different between muscles groups. The muscle volume, an important determinant of MVC, would explain the influence of absolute force on IET. Hypothetically, a greater muscle volume could be associated with elevated stored energy sources ([PCr], [ATP], glycogen, and oxygen bound to myoglobin) and consequently, a higher IET. Indeed, during whole-body exercise, Miura et al. (2002) showed a positive correlation (r = 0.59, p < 0.01) between W' and muscle cross sectional area of the thigh. In line with this data, Byrd et al. (2017) verified that local mineral-free thigh lean mass was significantly related with W' determined during cycle exercise. However, there is no study that has investigated the influence of muscle volume on IET. Thus, future studies should investigate the influence of neuromuscular characteristics (e.g., muscle volume, muscle fibre type) on IET during small-muscle-mass exercise.

Several lines of evidence indicate that critical power / ET is aerobic in nature, and consequently, influenced by oxygen delivery to the muscle (Kellawan et al. 2014). The ET expressed as absolute values was significantly higher for KE than for PF. However, ET expressed as relative values and normalized by MVC was significantly higher for PF than for KE. A smaller muscle force/volume has
been associated with lower blood pressure during isometric contractions, allowing increased blood flow and oxygen delivery to the muscle. Moreover, during whole-body exercise, it has been verified that critical power was correlated with muscle type I (r = 0.67, p = 0.025) and inversely correlated with muscle type IIx fibre proportion (r = −0.76, p = 0.01) (Vanhatalo et al. 2016). Thus, difference in blood flow and muscle type I distribution could explain, at least in part, a higher ET expressed as relative values for PF.

Finally, we acknowledge the potential limitation of using a single joint angle to compare MVC and exercise tolerance during small-muscle-mass exercise. The joint angle influences both MVC and exercise tolerance during submaximal isometric contraction (Boyas and Guével 2011), and consequently, the effects of muscle group on ET and IET could be muscle length dependent.

Conclusion

In summary, this study has demonstrated that during repeated submaximal isometric contractions performed at similar %MVC, exercise tolerance seems to be negatively influenced by absolute force. Above similar amplitude of ET, exercise tolerance is positively influenced by IET, which is partially explained by MVC, independently of muscle group. However, limit of tolerance during submaximal isometric contractions performed below ET is independent of IET. Thus, the limit of tolerance during small-muscle-mass exercise is influenced by absolute MVC only during exercise performed above ET, which seems to be explained by differences on both ET (expressed as %MVC) and IET values.
Conflict of interest

The authors report no conflicts of interest associated with this manuscript.

References


Burnley, M., Vanhatalo, A., and Jones, A.M. 2012. Distinct profiles of neuromuscular fatigue during muscle contractions below and above the critical


449 during severe-intensity exercise in humans: a 31P magnetic resonance
450 spectroscopy study. Exp. Physiol. 95(4): 528-540. doi:
Table 1. Mean ± SD values of maximal voluntary contraction (MVC), impulse above end-test torque (IET), and end-test torque (ET) for knee extensors (KE) and plantar flexors (PF) muscle groups. N = 40

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<th>IET (Nm·s)</th>
<th>ET (N·m)</th>
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<tr>
<td>KE</td>
<td>294.9 ± 62.5</td>
<td>7243.2 ± 1942.9</td>
<td>84.4 ± 24.8</td>
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<tr>
<td>PF</td>
<td>181.5 ± 37.6*</td>
<td>3357.4 ± 1132.3*</td>
<td>73.9 ± 19.5*</td>
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MVC - maximal voluntary contraction; IET - impulse above the end-test torque; ET - end-test torque; KE - knee extensors; PF - plantar flexors. * p < 0.05 in relation to KE muscles.
Table 2. Mean ± SD values of the exercise tolerance (s) obtained during the time exhaustion tests above (ET + 5%), below (ET - 5%) and at the same percentage of the maximal voluntary contraction (Similar %MVC) in relation to ET + 5% for PF. N = 11

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<tr>
<td>KE</td>
<td>611.7 ± 208.1</td>
<td>697.0 ± 243.7</td>
<td>1030.2 ± 495.4</td>
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<tr>
<td>PF</td>
<td>255.0 ± 78.6*</td>
<td>300.7 ± 156.7*‡</td>
<td>1028.3 ± 514.4</td>
</tr>
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KE - knee extensors; PF - plantar flexors. * p < 0.05 in relation to KE at the same exercise condition; ‡ p < 0.05 in relation to Similar %MVC condition.
Figure 1. Torque profile during submaximal isometric contraction for a representative subject. Arrow indicates first of three consecutive isometric contraction were the target torque was not attained. Dashed line represents the target torque.

Figure 2. Mean ± SD values of torque of knee extensors (KE) and plantar flexors (PF) during the 5-min all-out test. N = 40